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Epidemiology o

Plant-parasitic nematodes are not noted for causing devastating epidemics of plant disease. An outstanding exception is the pinewood nematode, *Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle (= *B. lignicolus* Mamiya & Kiyohara), the causal agent of pine wilt (7). This lethal disease of Japanese red pine (*Pinus densiflora* Sieb. & Zucc.) and black pine (*P. thunbergii* Parl.) in Japan has been epidemic in that country for over three decades. Primarily a mycophagous species, *B. xylophilus* is capable of colonizing the resin canals of a live pine and destroying their epithelial linings, resulting in cessation of oleoresin flow, disruption of the water transport system, and death of the tree within a few months after infection is established (6). The nematode is transmitted from dead to live pines by cerambycid beetles (8).

Pine wilt was discovered in the United States in Columbia, Missouri, in February 1979 (2). The report of that finding generated widespread interest in the disease and stimulated scientists across the nation to look for *B. xylophilus* as a possible cause of sudden and inexplicable decline and death of pines. In these few interim years, the nematode has been found in most states east of the Rocky Mountains and in California and has been recorded from 21 species of pine and six other conifers (3). Intensive interdisciplinary research on the pine wilt complex already has yielded important knowledge of the host-nematode-vector interrelationships in some areas of the country (1,5,10). The United States, however, has a vast array of both natural and man-made pine ecosystems, and the significance of *B. xylophilus* as an inhabitant of pinewood in most of these systems remains unclear.

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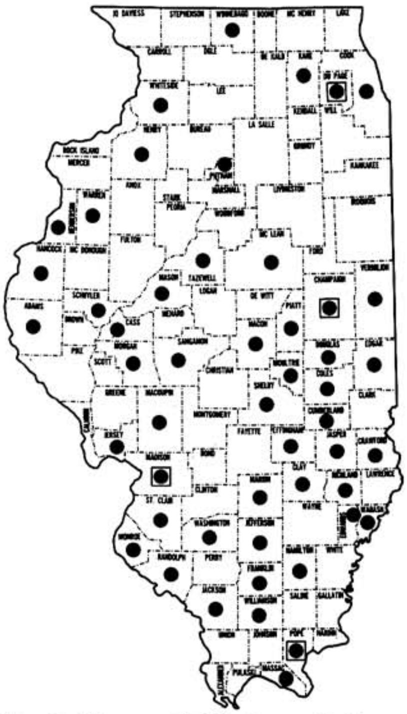


Fig. 1. Known distribution of *Bursaphelenchus xylophilus* in the 102 counties of Illinois. Each dot represents one or more detections. Dots within squares indicate initial sites of detection in the fall and winter of 1979–1980.

Published comparisons of the situations in this country and Japan conclude that pine wilt at present is not a significant problem in the native pine forests of the United States (3,9). On the basis of the history of pine wilt in Japan, however, Dropkin et al (3) expressed concern that the disease eventually could be a serious menace to pines in the United States. That possibility did indeed become a reality in Illinois, with a sudden outbreak of pine wilt in late 1979. The disease rapidly increased in incidence during the ensuing years and now is epidemic in introduced species of pine in many areas of the state. This article describes our experiences with the pine wilt complex and its various biotic components in Illinois.

Disease Distribution

Pine wilt was first recognized in Illinois near Collinsville, Madison County, in September 1979 (Fig. 1). *B. xylophilus* was recovered in large numbers from an Austrian pine (*P. nigra* Arnold) that had died suddenly in August. The tree was the first mortality in a 25-year-old residential landscape planting of mixed pine species. Four nearby Scotch pines (*P. sylvestris* L.) died by November. Several more scattered pine wilt losses of Scotch pine were found during the fall and winter of 1979–1980 on and near the Urbana-Champaign campus of the University of Illinois in Champaign County, at the Dixon Springs Agricultural Center in Pope County, and in the Morton Arboretum in Du Page County (Fig. 1). Prior to recognition of pine wilt, such isolated sudden losses had been attributed to individual or combined effects of other factors, including engraver beetles, Zimmerman pine moth, root rot and canker diseases, rodents, drought stress, adverse edaphic conditions, and lightning.

In the spring of 1980, a survey was begun to determine the distribution of *B. xylophilus* by county and the importance of pine wilt in Illinois. We, as well as county extension advisers, state district foresters and nursery inspectors, and landowners, collected wood samples from dead and dying pines at sites of suspected pine wilt incidence. The species of pine, its estimated age, the month symptoms appeared, foliar coloration at sampling, type of planting, year of first loss, and extent of incidence in the planting were recorded for sampled trees and sites. Samples were analyzed for presence of *B. xylophilus* at the University of Illinois Nematology Laboratory by soaking subsamples, usually branch disks, in water overnight. Exclusive of Champaign County, the number of sites sampled per county varied from one to 10 and did not reflect the extent of incidence within a county. Many sites sampled by cooperators were inspected, resampled, and photographed later by one of us (R.B.M.) to determine patterns of pine wilt development in localized areas.

Through 1982, *B. xylophilus* was

Pine Wilt in Illinois

detected in 50 of the 102 Illinois counties (Fig. 1). The nematode was recovered from virtually all pines that had shown the characteristic symptoms of sudden whole-tree death or branch mortality preceding tree death. Resampling sometimes was necessary to reveal nematode infections. At several locations, the L_{III} dispersal stage of the nematode (7) was found in trees that had died up to 3 years earlier. Though county detections now are rather evenly distributed through much of the state, generally they occurred earlier in the southern third, where incidence of pine wilt was more widespread and locally intense. The disease has been reported from additional counties in southern Illinois, but the presence of *B. xylophilus* has not been verified.

Over 300 cases of pine wilt, representing only a small fraction of actual losses, were confirmed during 1980–1982, and 85% of these were in Scotch pine, the dominant landscape, windbreak, and Christmas pine in most areas of Illinois. Disease incidence was much less in Austrian and red (*P. resinosa* Ait.) pines and rare in eastern white (*P. strobus* L.) and mugo (*P. mugo* Turra) pines, other commonly planted species. The disease also was encountered occasionally in loblolly (*P. taeda* L.), jack (*P. banksiana* Lamb.), and Virginia (*P. virginiana* Mill.) pines. Outside the genus *Pinus*, the nematode was found only in single 12-year-old specimens of blue spruce (*Picea pungens* Engelm.) and Douglas-fir (*Pseudotsuga menziesii* Franco), both of which were in an area of high wilt incidence in Scotch pine and died suddenly in late summer.

Pine wilt has occurred most commonly in landscape and windbreak plantings (Fig. 2), where increasing numbers of trees have succumbed annually. Concentrated plantings of Scotch and Austrian pines have suffered up to 25% loss. The disease first appeared in a random pattern of single isolated cases. As incidence increased, groups of two or more adjacent trees frequently died over a period of 1–2 years. In multirow plantings, the disease often occurred initially in the interior and was not detected until peripheral trees became afflicted. Where pine wilt has become well established, mixed plantings of susceptible Scotch pines and apparently resistant, healthy white pines present striking contrasts.

Table 1. Two-year chronology of pine wilt losses in Scotch pine in the Urbana-Champaign area of Illinois

Year	Number of mortalities by month[a]												Total
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
1980	0	0	2	3	10	0	0	10	23	12	5	0	65
1981	0	0	10	10	15	4	2	3	7	3	1	0	55

[a] Based on first visible change in overall foliar coloration.

Incidence of pine wilt has been greatest in rural environments, but urban and suburban areas have also experienced substantial losses. Many Scotch pines that provide a protective overstory for *Rhododendron* and *Azalea* spp. in the Morton Arboretum have succumbed. The disease was identified in seven of approximately 300 active Christmas tree plantings and in five abandoned plantings. It was confirmed in four major pine plantations on public land, including one of two 2,000-tree Scotch pine provenance plantations. These large, widely separated plantings containing standing dead pines represent continuing natural sources of both nematodes and vector beetles for much of the state. Pine wilt first became established in these plantations or overage Christmas tree plantings, then spread to surrounding windbreaks and finally into urban areas.

Most cases of pine wilt have occurred in trees 15–25 years old, the approximate median age of landscape and windbreak Scotch and Austrian pines in Illinois. Many plantings are located along interstate highways where dead trees are highly visible. Incidence has been rare in younger pines, except in Christmas tree and nursery plantings, where trees as young as 8 years have died. Sources of infection for these young, high-density plantings, in which dead trees normally are culled, were traced to older dead pines nearby. Loss of aesthetically high-value pines over 50 years old, though increasing, has been relatively low because most are located sparingly in cemeteries and around isolated farmsteads.

Local Epidemic

An epidemic of pine wilt began in the Urbana-Champaign area in 1980 and was monitored closely for 2 years (Table 1). Through 1981, *B. xylophilus* was recovered from 120 Scotch and six Austrian pines that had died or were showing initial symptoms preceding death. Most had been in good condition, and some were among the oldest and most stately pines in Illinois (Fig. 2E). Several dozen additional nonsampled but apparent losses to the disease occurred among Scotch pines in the vicinity of sampled trees. The number of confirmed cases during the low climatic stress year of 1981 was somewhat lower than during the high stress year of 1980. Losses continued at a similar pace in 1982, despite an urban and suburban sanitation program to destroy dead pines during the preceding years.

The epidemic centered on the campus of the University of Illinois and was most intense in concentrated landscape plantings of Scotch pines 15–20 years old. In one planting of 400 trees, 15% had died by the end of 1982. Probable sources of infection for the epidemic were a rural 30-year-old multispecies pine plantation on the University South Farms and an 80-year-old Scotch pine planting in a cemetery near the center of the campus. Both sites contained standing trees that had died 1–3 years earlier, showed evidence of cerambycid borer activity, and harbored *B. xylophilus*.

The first incidences of pine wilt on campus were traced by trunk and stump sampling, extrapolation, and photographic records of the University Operation and Maintenance Division back to 1979, when a few scattered Scotch pines had died from a then unknown cause. Tree deaths resumed in the spring of 1980 and greatly increased toward late summer. Isolated losses from pine wilt began in windbreak, residential screen, and specimen plantings of Scotch pine in suburban and rural areas up to 8 km from the campus and the South Farms plantation during 1980. Incidence in these areas intensified during 1981. Dead windbreak trees usually were left standing and became heavily infested with cerambycid borers, virtually nullifying efforts to control the disease in other plantings through sanitation.

Symptomatology

Symptom development followed a rather unique and systematic pattern during the 2 years of closely observing the many Scotch pines 15–80 years old and the several Austrian pines 30–80 years old afflicted with pine wilt in the Urbana-Champaign area. There were two general periods of tree death, late winter to late spring and midsummer to late fall (Table 1). These periods were well delineated in 1980, which had a normal spring but an abnormally hot, dry summer with heat unit accumulation (HUA) much above normal into autumn. Mortalities began in mid-March and peaked distinctly in early May and again in early September. No trees died in June or July. In 1981, the first mortality period began in early March with greater intensity than in 1980, following midwinter thaws that had not occurred during the previous winter. Mortality peaks were less obvious during this contrasting, low-stress year with HUA much below normal into autumn. A few trees died during June and July, and the second period was much less intense than in 1980. The variations in seasonal incidence between years probably were related to the 550 C difference in HUA (base 18 C) through the growing seasons.

The most dramatic symptom of pine wilt in Scotch pine was a change in overall foliar coloration, which developed most rapidly and uniformly through the crown in August and September and in trees of compact form. During the warm months, the color change progressed through four relatively distinct stages (Table 2). Stage 1 was a light grayish green discoloration (Fig. 2C,J,K), which appeared abruptly, was first detectable in low-contrast light, and was accompanied by a cessation of resin flow from the wood. Stage 2 was yellowish green (Fig. 2D,L), stage 3 was yellowish brown (Fig. 2C,M), and stage 4 was light chocolate to rusty brown (Fig. 2D,E,N). The change from normal green to stage 4 occurred within as little as 1 month during hot weather. There was not the obvious needle wilt characteristic of the disease in longer, finer needled species of pine (6). Except for very large trees, *B. xylophilus* could be found, often in abundance, in virtually all trunk and branch samples from August and September mortalities showing advanced symptoms.

The change in foliar coloration slowed and became nonuniform over the tree with lower temperatures in autumn. Death of trees ceased in late autumn. Flagging (death of individual branches) began in mid autumn and continued into December. *B. xylophilus* could be recovered from branch flags but not from lower trunks or from most live branches. The flag showed the same four stages of foliar color change as observed when the entire tree died. The change progressed slowly, reaching stage 4 during the winter months. Small terminal winter flags (Fig. 2F) resembled summer flags induced by canker organisms but lacked the resinous exudation on the bark. Flagging had no pattern of location in the tree and varied from a single branch (Fig. 2F), possibly the site of transmission, to as much as 50% of the crown (Fig. 2E,G–I). This partial tree death was most distinct in a pine with twin leaders but with only one leader infected and with no nematodes detectable in the main trunk (Fig. 2I).

Trees with winter flags died in the spring as temperatures rose. In general, the lower the flag(s) in the crown, the greater the degree of flagging, and the younger the pine, the earlier the tree died during this period. Infected trees sometimes showed no symptoms into winter but developed one or more flags in late winter or early spring and died within a few months. Even after symptoms had progressed from flagging to overall foliar discoloration, *B. xylophilus* often could be found only in butt sections of originally symptomless branches.

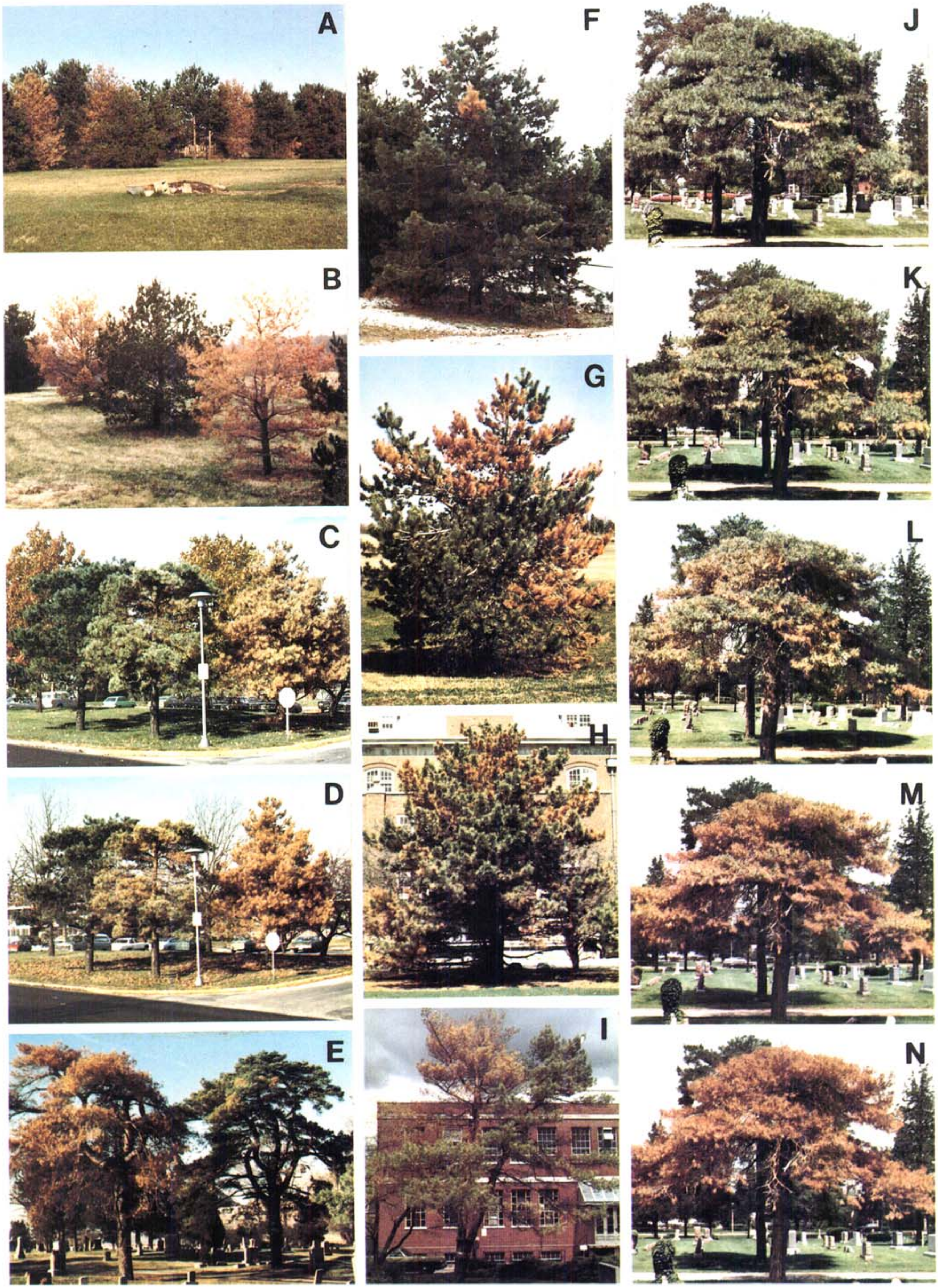
The change in foliar color in spring varied from rapid and uniform to gradual and asynchronous, with all four stages initially represented in the crown. A distinct wilt of candles often accompanied the onset of foliar coloration symptoms in early spring mortalities. Trees that died in mid to late spring usually showed interrupted new growth initially and the color change in the second- and third-year needles first. Tall, spreading old trees with widely separated limbs died more slowly during this period, symptoms spreading gradually through the crown from the initial flag. Rarely, old trees showed a progressive downward branch decline over a period of up to a year from the appearance of a flag at the top of the crown.

Dead pines retained most of their needles for 6–12 months (Fig. 2A,B,E), depending on age, season of death, and location. Needles remained longer on

Table 2. Sequence and duration of stages of symptom development in pine wilt of Scotch pine in summer mortalities

Stage	Duration	Symptom	Figure
1	1–2 weeks	Light grayish green foliage, sudden appearance; resin flow in wood ceases	2C,J,K
2	1–2 weeks	Yellowish green foliage, random needles brown; branch wood no longer resinous	2D,L
3	2–3 weeks	Yellowish brown foliage, random needles still light green; bluestain obvious in wood	2C,M
4	6–12 months	Totally brown foliage, needles retained without obvious droop; heavy bluestain in wood	2D,E,N; 3

Fig. 2. Patterns of incidence and symptom development in pine wilt in Illinois. (A) Rural Urbana, 20-year-old Scotch pines. Typical appearance of a windbreak with high incidence of the disease; several earlier mortalities were removed. (B) Rural Massac County, 15-year-old Scotch pines. Symmetry disruption of a uniform, single-row driveway landscape planting. (C and D) Suburban Urbana landscape planting, 20-year-old Scotch pines: (C) Late September—healthy (left) and two late summer-fall mortalities in stage 1 (center) and stage 3 (right) of foliar color change; (D) late October—afflicted pines now in stage 2 (center) and stage 4 (right). (E) Urban Urbana cemetery planting, 80-year-old Scotch pines, mid-December. August mortality (left) and several winter flags in the upper crown of a subsequent spring mortality (right). (F) Rural Urbana windbreak-screen planting, 20-year-old Scotch pine, late February. Single *Bursaphelenchus xylophilus*-infected winter terminal flag; tree remained healthy after entire branch was removed. (G) Suburban Urbana, 15-year-old Scotch pine, mid-March. Multiple winter flags; tree died in mid spring. (H) Urban Urbana, 40-year-old Austrian pine, mid-March. Multiple winter flags; tree died in early spring. (I) Urban Urbana, 40-year-old Scotch pine with twin leaders, early April. Dead, nematode-infected left leader and live right leader uninfected through winter (lower left limb emanates from right leader); tree died in mid spring. (J-N) Urban Urbana cemetery planting, 60-year-old Scotch pine (dead branch in center not associated with pine wilt; upper crown of healthy pine shows in background): (J) Late May—early stage 1 of foliar color change, (K) early June—late stage 1, (L) mid-June—stage 2, (M) late June—stage 3, (N) early July—stage 4.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young pines that had been growing rapidly than on isolated mature trees that were more exposed to high winds. Trees that died in spring generally shed their needles in autumn, whereas those that died in the summer-fall period shed during the following summer. Needle-shed from flags preceded that from the rest of the tree.

During their seasonal periods of activity, cerambycid and scolytid beetles often began ovipositing in infected trees before the onset of foliar symptoms. By autumn, frass of cerambycid larvae usually became abundant in branch crotches and beneath bark of trees that died from spring through later summer. Most fall mortalities escaped cerambycid infestation until the next summer. Beetles avoided these trees when more recent mortalities were available.

The sampling procedure for detecting *B. xylophilus* in a wilt-afflicted Scotch pine required critical attention to size and shape of the tree, type of symptom expression (flagging vs. overall), stage of foliar symptom development, and season of death. The nematode was recovered in population densities up to 20,000/g of wood (dry wt) from sections of branches from dead, needle-bearing pines. It often was abundant in roots down to 2 cm in diameter and up to 2 m from the bases of young trees in stages 3 and 4 (Fig. 2A–D). Conversely, it seldom appeared in lower trunks of tall old pines (Fig. 2E) until the trees had been in stage 4 for several months, and then only as the dispersal larva. The nematode was detected easier and usually in higher populations in trees that died during the summer-fall period. Though present in trunks, it frequently was absent from branch wood at any stage of symptom development in spring mortalities. It was never found in needles and cones and was rare in terminal twigs.

Adults and propagative juveniles of *B. xylophilus* were recovered from infected trees up to a year after first appearance of flags. The dispersal stage was rare in winter flags and newly killed trees but became the dominant form as the wood dried, appearing first in small-diameter branches. It usually was the only form present by summer in trees that died during the preceding summer-fall period and by winter in spring mortalities. The dispersal stage was recovered in declining numbers from the trunks of standing pines up to 3 years after tree death. Nematode populations were pure *B. xylophilus* until scolytid and cerambycid beetles infested the wood, after which many other insect associates were encountered.

Bluestain fungi (*Ceratocystis* spp.), on which *B. xylophilus* readily reproduced in agar plates and which reportedly sustain the nematode after tree death (7), rapidly invaded the wood of August and September pine wilt mortalities. Staining was first visible as a single triangular wedge expanding radially from the center to the exterior of cross sections from branches as early as stage 2. Staining became obvious by stage 3 and frequently involved more than 50% of trunk and branch cross sections by stage 4 (Fig. 3). Bluestain seldom occurred in wood of the last fall mortalities and the winter flags. It appeared very slowly in spring. *B. xylophilus* frequently could not be isolated from nonstained sections of branch wood from spring deaths.

The disease syndrome in Scotch pine apparently is the same wherever pine wilt occurs in Illinois and closely resembles the syndrome in Japanese black and red pines in Japan (6). Dissimilar or unreported etiological aspects observed in Illinois include: 1) two annual periods of tree death, 2) absence of obvious wilting of needles, 3) branch flagging of live trees during the cool months, 4) nonsystemicity of nematode populations in spring mortalities, and 5) absence of nematodes from needles and cones. Variations may be due to climatic differences between Illinois and Japan. The inevitable death of flagged Scotch pines with verified infections substantiates that trees of this species are doomed once *B. xylophilus* becomes established in the wood. The trees apparently do not succumb to the disease, however, until the nematode populations become widely dispersed in the trunks.

Symptom development in Austrian pine appears to be similar to that in Scotch pine but somewhat slower. Early diagnosis based on symptoms is complicated in Austrian pine by its high susceptibility to Diplodia dieback, in which symptoms often are superficially similar to those of pine wilt. Moreover, large numbers of an *Aphelenchoides* sp., which probably feeds on the fungus and may be confused with *B. xylophilus*, frequently are recovered from branch sections from blighted Austrian pines. The syndrome in other species of pine is unclear because of relatively low pine wilt incidence and frequent difficulty in locating *B. xylophilus* infections in trees.

Nematode Pathogenicity

We have demonstrated pathogenicity of *B. xylophilus* in several tests on Scotch

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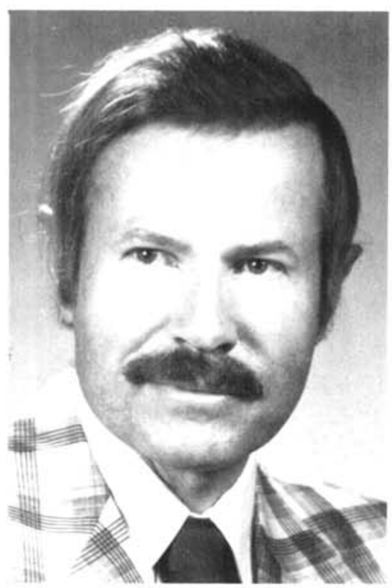

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pines 2–4 years old (*unpublished*) by pipetting nematodes into absorbent cotton taped around a shallow notch in the stem or into rubber tubing affixed to the butt of an excised lateral twig. Either method establishes infection, but the latter is simpler and faster. Separate inoculations with dispersal-stage larvae from a dead Scotch pine, dauerlarvae from a sawyer beetle, and multiple-stage propagative nematodes cultured on *Botrytis cinerea* Pers. all have resulted in death of young trees. The pathogenicity of *B. xylophilus* in established pines, however, has not been demonstrated adequately. Perhaps of greater importance, the disease incubation period, which may heavily influence strategies for saving infected trees, has not been determined. Trunk inoculation of 20-year-old Scotch pines at Urbana in July 1981 after spring growth had been completed resulted in death of only two of 18 trees, early the next spring.

B. xylophilus monoxenically cultured on *Botrytis cinerea* infected and ultimately killed 75–90% of sturdy 3- to 4-year-old Scotch pines inoculated with 1,000 nematodes during the June period of rapid tree growth and incubated under greenhouse conditions ($\bar{x} = 25$ C). Up to 6,000 nematodes per gram of stem wood (dry wt) were recovered from recently killed trees. Infected trees usually died 3–6 weeks after inoculation. The rapid and uniform overall change in foliar coloration in most of these mortalities was virtually identical to pine wilt symptom development in older established trees during late summer and early fall. The change frequently was preceded by wilt of candles, noted in some field mortalities in the spring. Symptoms on the few trees that died 2–3 months after inoculation appeared first on one or more lateral twigs or on one of two leaders, resembling the branch flagging often encountered in infected field trees in late fall and early spring. For unknown reasons, infections did not become established in some June-inoculated pines and in most trees inoculated from July to September, after candle and needle elongation had been completed.

B. xylophilus readily dispersed from inoculated to noninoculated 4-year-old Scotch pines via temporary stem grafts, killing both donor and receiver pines. Intratree-branch grafting is common in multiple leader Scotch pines, as is intimate intertree-branch contact and resulting abrasion wounding among closely growing pines. The ability of the nematode to migrate between experimentally grafted young trees implies an alternate, nonvector means of natural local dispersal within and among Scotch pines. Root grafting also occurs in older pines and may provide a similar route of intertree dispersal, as the nematode often becomes distributed well into the root systems of infected pines.

Vector Distribution and Transmission

Virtually nothing was known of the Illinois distribution and biology of the pine sawyers (*Monochamus* spp.), the beetle adults of which are the presumed primary vectors of *B. xylophilus*. Until the discovery of pine wilt, they were considered of no economic importance in the state. Only a few specimens of *M. carolinensis* Oliv. and *M. titillator* F., collected in southern Illinois in the early 1900s, were deposited in the Illinois Natural History Survey Museum. Larvae of sawyer beetles or their frass and tunnels now are found in dead pines wherever pine wilt is encountered.

The sawyers dominate the cerambycid fauna of wilt-killed pines in Illinois. All sawyer beetles reared from dead, naturally infested wood from widely separated locations in 1981 (550) and 1982 (485) were *M. carolinensis*. Infested trunk and branch wood from one 20-year-old Scotch pine from Urbana yielded 185 beetles. In both years, over 90% of dissected sawyer beetles that emerged in June and July from wood of *B. xylophilus*-infected trees at three sites in northern, central, and southern Illinois were infected with dauerlarvae of the nematode in numbers up to 90,000/beetle ($\bar{x} = 21,000$). Among other cerambycids that emerged from the wood, *B. xylophilus* was found only in a few specimens of *Amniscus sexguttatus* Say from a red pine in numbers up to 700/beetle. Scolytid beetles that heavily infested diseased trees did not carry the nematode, even though the dispersal stage often was abundant in frass around the beetles beneath the bark.

We have shown in vector tests initiated in June and July that *M. carolinensis* will transmit *B. xylophilus* to Scotch pine (*unpublished*). Frequency of transmission, however, was relatively low (<30%) in all tests. Nematode dauerlarvae and adults were recovered from twigs excised from healthy plantation pines and exposed to beetles for maturation feeding for 1 week. Trees 3–4 years old became infected when exposed to beetles under greenhouse conditions and died within 2 months. Beetle feeding alone severely injured candles, twigs, and stems, often killing upper crowns. Transmission to two of seven 20-year-old trees resulted in autumn flagging of branches on which beetles were caged and death of trees in early spring.

Conclusions

Pine wilt has been considered endemic but not epidemic in the United States (3). In Illinois, the disease apparently was not endemic and did not occur north of the Shawnee National Forest near the southern tip of Illinois until recent years. Despite rising public awareness of the disease, recent historical evidence shows convincingly that pine wilt has been increasing rapidly in both distribution and local severity in Illinois: 1) its appearance since 1979 in areas where no sudden pine deaths had occurred earlier and in a generally more northward pattern, 2) the increase in incidence in plantings with verified prior infections, and 3) the sudden occurrence of local epidemics between 1980 and 1982. Moreover, incidence of the disease obviously is far more widespread and locally intense than the number of verified cases would indicate. Many plantation blocks, abandoned Christmas tree plantings, and field windbreaks are in isolated locations where the disease is easily overlooked.

Several interrelated factors are thought to have caused the rapid increase in importance of pine wilt in Illinois: 1) widespread planting of two highly susceptible introduced pine species, 2) enhanced branch mortality and general decline of pines resulting from stress on trees from the severe winters of 1976–1979 and more recent summer droughts, 3) consequent creation of more favorable habitat for sawyer beetle breeding in a mostly prairie region to which the vector presumably had not been native, 4) explosive increase in beetle populations with the increasing number of pine mortalities, 5) failure to remove and destroy dead, nematode-infected pines before beetle emergence, 6) rapid rise in the number of susceptible-age pines in recent years, 7) expanded high-density planting of Christmas trees and their ready access to the vector for maturation feeding, and 8) postharvest abandonment or poor maintenance of plantings left to mature for pulp production, wildlife cover, or aesthetic value.

Two very different systems involving *B. xylophilus* may be operating in the United States, as is indicated in the north central states. In the natural conifer belt of the upper part of the region, the pines are primarily native species that are relatively resistant to the nematode (3–5) and grow under minimal abiotic stress. There, *B. xylophilus* has been found only in pines apparently stressed or killed gradually by forest insects and diseases and already colonized by potential cerambycid vectors, the typical symptoms of pine wilt have not been observed, and the nematode may be only a secondary invader transmitted to dead wood during beetle oviposition (9,10). A distinctly contrasting situation exists just a few hundred miles to the south in Illinois and portions of surrounding prairie states, where pines are mostly offsite-planted, consist largely of susceptible introduced species, and often are exposed to relatively high abiotic stress. Here, untold

Fig. 3. Heavy *Ceratocystis* bluestain observed in late November in the trunk of a *Bursaphelenchus xylophilus*-infected Scotch pine that had died in late August.

thousands of well-established pines have died suddenly within the last few years after surviving many severe winters and droughty summers. Most had been in relatively good condition and free from significant stress from insects and fungal diseases. The constant association of *B. xylophilus* with Scotch pines showing the characteristic symptoms of pine wilt and the rapid nematode kill of vigorous young trees in pathogenicity tests provide strong evidence that the nematode is a primary, rather than secondary, invader of these pines. The association in killed established trees exists whether or not *M. carolinensis* and other cerambycids have infested the trees. Deaths occur both within and outside the annual period of beetle activity and in years of low or high summer abiotic stress. Highway travel through areas of extensive plantings of susceptible pines and close observation of the numerous local epidemics in Illinois show convincingly that pine wilt is a serious and growing problem. The apparently disparate systems in the north central region may exist in other regions of the country where there is similar wide divergence in the ecology of pines.

Pine wilt has emerged within a very few years to become the most destructive of all pine diseases in Illinois. Its rapid increase in incidence resembles the earlier epidemic spread of Dutch elm disease through the state, the two diseases having several aspects in common—rapid death of susceptible hosts, beetle vectorship of the pathogen, and involvement of *Ceratocystis* fungi. Pine wilt now poses a serious threat to the more susceptible species of pine, particularly to the vast number of Scotch pines in landscape, windbreak, and Christmas tree plantings. Eradicating the disease locally and minimizing the incidence statewide require a thorough program of sanitation to eliminate the breeding habitat of the sawyer beetle vectors. The success of the program, however, depends on extensive public awareness of this recently detected disease and of the importance of destroying dead pines before annual vector activity begins. As was the case with Dutch elm disease, public negligence, storage of felled infected trees for firewood, overlooked mortalities, and forest infections will reduce the effectiveness of sanitation by providing continuing sources of nematodes and vectors. Extensive plantations and natural forests of pines, where sanitation procedures are impractical, pose a particularly serious problem for containment of the disease. The current lack of an effective means of controlling the vector in these situations renders prevention of spread to nearby high-value plantings virtually impossible.

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